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ON THE HABITAT OF THE EARLY VERTEBRATES

IF we take the record as it stands, the appearance of the fishes, the first known vertebrates, is one of the most abrupt and dramatic in the life-history of the earth. They seem to come trooping on the stage of action from some concealed source in full company and clothed in varied and curious armor, and at once a battle scene of prodigious range and duration begins. There had been some feeble premonitions, but these had revealed little of the coming drama. That there had been a long series of preliminary trainings, with trials and changes of armor, and rehearsals, and shiftings of parts, we cannot doubt, but where and how this transpired has been an unsolved mystery, though we have tried industriously to get behind the scenes.

The trivial premonitory signs of the apparition, even when interpreted by retrospective light, only serve to render their meagerness the more singular. If the fishes were armored in the Ordovician period, as the Colorado relics found by Walcott seem to show, and if these mail-clad fishes continued to live in the seas and to develop into the panoplied host that made its apparition during the transition stage from the Silurian to the Devonian, why did they not leave a more fitting registration of their presence? The "imperfection of the geological record" is indeed great, but in seas that preserved soft medusæ and delicate graptolites, it would seem that armored fish should have left abundant and substantial signs of themselves, if they were there. The Trenton relics of Colorado, if taken at their fullest assigned value, help to make such a record, it is true, but at the same time they emphasize its scantiness and nullify the familiar appeal to an unfossilizable softness of structure and perishableness of parts. While they contribute a little to the record, the chief effect of their discovery is to greatly strengthen the opinion long entertained that the fishes must have had a very protracted

pre-Devonian history, and to reënforce the conviction that the evolution of full suites of armor and varied forms of dentition was the work of a prolonged period and had almost necessarily many fossilizable stages previous to the striking display in the Devonian period and this conviction becomes the more firm when it is considered that the differentiation and the armoring extended not only to many different orders, but to subclasses and even classes. If Walcott's interpretations be accepted to relieve the dearth of the record, they must also be accepted as showing susceptibility to fossilization so much the earlier.

As the record now stands, there are fragments of plates, scales, and a supposed notochord from the Trenton of Colorado; but a dearth everywhere else in the widespread and well-studied Ordovician and throughout the early and middle Silurian. Then, in the transitional stages from the Silurian to the Devonian, fish remains appear on both continents, and before the Devonian has passed, they present a rich and varied deployment, embracing not only the two classes *Agnatha* (jawless fishes, *Cyclostomata*) and *Pisces* (true fishes) but all the known subclasses of these and a majority of their orders, according to the most recent authoritative classification.

The physical and biological associations of this extraordinary deployment were peculiar. On neither continent do fish remains appear abundantly in the open sea deposits. They are confined chiefly to the sediments of inland waters or of littoral zones or of embayed arms of the sea. The fish of the Corniferous limestone, perhaps most nearly an exception to this generalization, may properly be put in the last class, for the Corniferous beds were laid down in a great bay with only limited connection with the sea, though the fauna was truly marine.

In the Ludlow "bone bed" of England, where they first make their appearance in abundance, the fish remains are associated with Eurypterids, probably the most gigantic Crustaceans that have ever lived, some of them attaining two meters in length. There is the same association on the continent, notably in the island of Oesel in the Russian Baltic and in Podolia and Galicia,

and so again in the Waterlime group of America in which the *Pteraspis Americana* of Claypole occurs. The physical conditions in all these cases seem to have been peculiar, and in the case of the Waterlime group they were singularly so, for they permitted a host of these large Eurypterids and other Crustaceans to flourish in seeming luxuriance, while only a meager and pauperate marine fauna found an occasional entrance into the series. The conditions seem to have been congenial to the fish and Eurypterids but not to a typical marine fauna.

In the Old Red Sandstone phase of the Devonian both in Europe and America a similar association obtained. A most extraordinary group of fishes and a family of most gigantic Crustaceans flourished where marine life found only an occasional and meager presence. These few marine forms, here and there in a massive deposit, no more imply prevalent salt water than the present marine species in the Bay of San Francisco imply that the gravels, sands and silts of the valley of California and of the Great Basin, which seem to be analogues of the Old Red Sandstone, are prevaillingly marine. The further association of the fishes and Eurypterids with land plants and fresh water mollusks, together with a total absence of marine relics from the same beds, leaves no solid ground for hesitating to accept the dominant view of English and other geologists that the typical Old Red Sandstone and its homologues are the deposits of fresh waters and that both the fishes and the Eurypterids found congenial conditions of life in them. As fishes and Eurypterids were found both earlier and later in marine deposits the question arises: *Were the fishes and Eurypterids primarily marine and later became adapted to fresh water, or were they primarily fresh-water forms which were occasionally carried out to sea, and which later became adapted to salt water?* The two cases do not necessarily require an identical answer, but the singular association of the two in unusual display under peculiar conditions and on both continents strongly implies a community of habit, at least at the stages in question. The association is one of the most unique faunal and physical combinations of geologic history.

The earlier occurrence of the Eurypterids in marine deposits is almost as limited as that of the fishes, and yet they were well adapted to fossilization and were actually fossilized as far back as pre-Cambrian times, as Walcott has recently shown by their discovery in the Belt Mountain terrane of Montana. Of about a dozen known genera of Eurypterids, only two or three of those least well known are without associations with formations regarded as fresh water. The relics found in marine sediments may be attributed to transportation from the land just as is done in the case of the terrestrial plants and land insects not infrequently found in marine beds; but transportation in the opposite direction cannot be assigned. In the Ordovician but a single Eurypterid representative is known to occur and of this very little is known. In the pre-Cambrian beds of Montana a more abundant presence seems to be indicated, but little has yet been learned of the concurrent physical conditions. The thousands of Crustacean fragments are associated with a few trails assigned to annelids and some that are possibly molluscan or crustacean, and the inference is that the deposits were made in the sea. From the occurrence of Eurypterids first in marine beds apparently and later in fresh-water deposits it has been inferred that they were originally sea-dwellers and later became adapted to landwaters, but the meagerness of their marine record on the one hand, and their abundance and fine preservation in the fresh-water deposits on the other, give point to the question whether their early marine record is anything more than the chance deposit of river forms borne out to sea. When it is considered that the records of acknowledged marine types are, on the whole, good as such things go, and have been widely and well-studied, there is an incongruity in the case of both the fishes and the Eurypterids between the meager marine records of the Ordovician and Silurian, and the impressive fresh-water record of the same forms in the Old Red Sandstone phase of the Devonian, and this incongruity may well be regarded as significant.

There is reason to believe that opinion has been much influenced—more or less unconsciously no doubt—by general

presumptions, rather than specific ones. There is a strong general presumption, based on theory and observation, that the earliest life was marine and hence that in the gross the course of migration has been from the sea to the land and to the air. But this should weigh nothing in particular cases not in conflict with it, for the descent of reptiles and mammals from the land to the sea is well established, and this in no way contravenes their remote ascension from a marine ancestry. It may be equally true that the fish and the Eurypterids descended from the rivers to the sea in the mid-Paleozoic, though their remote ancestors may have ascended from it.

In dealing with the specific presumptions of the case it is to be noted that the relics of river faunas are imminently liable to be borne down to the sea, while transportation in the opposite direction is unassignable. The presumption is that a land or fresh-water fauna will be somewhat represented in contemporaneous marine sediments if it be readily fossilizable. The fragments of fish and Eurypterids in the marine beds previous to the transition stage at the close of the Silurian are not more than could be expected if fish and Eurypterids were living in the streams of those times, but entirely absent from the seas. Indeed the record is rather scant even on this assumption.

A more or less widely accepted presumption regarding the early states of the land has possibly also weighted against the hypothesis that the fishes had their early development in the land waters, viz., the presumption that the land was without vegetal clothing, and that hence its waters were sterile and unsuited to life. Against this presumption there are several important considerations. If the land were naked, not only would the streams be sterile and silty from the unrestrained wash of the surface, but the waters of the sea border would also be similarly affected in some notable degree. Sea life should have avoided rather than sought the sterile, silty, shore waters. But the abundance of littoral life in the early Paleozoic fails to support this view.

Moreover, if the land were unprotected by vegetation, the rate of transportation of loosened surface materials would probably have been too great to permit complete chemical disintegration. As fast as crystalline grains were separated from their fellow grains by disintegration acting at their contacts, or along cleavage planes, they would doubtless have been promptly carried away to sea and the sands and silts would have been arkose in type. But as far down as the Cambrian at least they are distinctly not so, as a general rule. They are as pronouncedly disintegration-products as in any later age. The Upper Cambrian sandstone of the American interior is a most typical example of a thoroughly disintegrated product. The Huronian series, as developed about the Upper Great Lakes, bears scarcely less distinctive evidence of the dominance of disintegrating agencies than the Mesozoic and Cenozoic terranes on whose origins the influence of an ample clothing of vegetation wrought its full effects.

Still further, the voluminous carbonaceous deposits of the Huronian give support to the assumption that at least lowland vegetation then prevailed in abundance. These carbonaceous deposits have been compared in respect to the amount of carbon with the coal beds of the Carboniferous and Cretaceous periods, and not without some show of justice.

There are good reasons therefore for displacing the presumption, rather current in the earlier half of the century, that the lands of the older Paleozoic periods were barren of vegetation and for the substitution of the presumption that land vegetation was prevalent as far back as the shore deposits display the residuum of complete disintegration and abound in the relics of sea life. Beyond that, where the schists do not radically differ in chemical constitution from the igneous rocks, the era of a naked earth and the reign of disaggregation with slight decomposition may be placed amid the other mysteries of the Basement Complex.

The richness of littoral marine life, at least as early as the Cambrian, the carbonaceous deposits of the Huronian and the

chemical nature of all the Paleozoic and most of the Proterozoic strata, afford, in my judgment, ample ground for the presumption that vegetation clothed the land from a date long anterior to the Paleozoic era and that the land waters were capable of supporting their own appropriate fauna, as well as contributing to the support of that of the sea border.

Now there is one distinctive characteristic of land waters that deserves consideration in the study of the evolution of the early vertebrates, because it was a strenuous dynamic condition constantly impressed upon their fauna. It is their most familiar and essential feature, *their flow*. Neglecting lakes, which are mere incidents, land waters are distinguished by persistent and usually rather rapid motion in a fixed direction, and this is an insistent physical condition to which their fauna must adapt itself. Fortunately this adaptation must take a tangible form, whereas adaptation to the freshness of the water is accomplished by obscure modifications which are not as yet detectable. In flowing water, the animal must maintain its position against the current either by a contact of some resisting kind with the bottom of the stream, or must be provided with an effective mode of propulsion competent to meet the constant force of the current without undue draft on the vital resources; otherwise the animal would be swept out to sea and its race be ended as a stream-dweller. It is different with ocean currents, for they return upon themselves and an animal may yield to them without losing its marine habitat; and besides, they are usually much feebler than river currents.

A glance at the faunas of existing streams, which represent the outcome of ages of trial, shows only three prominent groups of animals that have accomplished the adaptation. The minor instances are negligible. The successful cases are, first and foremost, fish, second, certain mollusks that crawl on the bottom with firm contact, and third, certain crustaceans that are provided with numerous sharp claws that give them ready catch and hold upon the stream bed. The brachiopods that are free in youth, but sessile or pediceled in later life, the cephalopods that are

floating or swimming forms, the corals, the chrinoids, the echinoids, and many other sea forms of ancient history and long opportunity, have not made an effective entrance into the streams during geologic time; and this is probably not wholly, and perhaps not chiefly, due to the sweetness of the waters.

A compact form of body presents obvious advantages, except as environment or food or locomotion requires some departure from it, and the vast majority of animals are more or less rotund, and their locomotive devices are adjusted to this form. But the rotund form offers much resistance to rapid currents and unfits the animal for effective stream life unless it persistently hugs the bottom. Neither the rotund floaters and swimmers like the ancient cephalopods, nor the ciliated spawn of the sessile forms are well adapted to resist the unceasing pressure of a rapid stream, and these are practically absent from river faunas.

There is only one conspicuous type that is facilely suited to free life, independent of the bottom, in swift streams, and that is the fish-form. The form and the motion of the typical fish are a close imitation of the form and motion of wisps of water-grass passively shaped and gracefully waved by the pulsations of the current. The rhythmical undulations of the lamprey which perhaps best illustrates the primitive vertebrate form, and is itself archaic in structure, are an almost perfect embodiment in the active voice of the passive undulations of ropes of river *confervæ*. The movement of the fish is produced by alternate rhythmical contractions of the side muscles, by which the pressure of the fish's body is brought to bear in successive waves against the water of the incurved sections. In the movement of a rope of vegetation in a pulsating current, it is the pressure of the pulses of water against the sides of the rope that give the incurvations. The two phenomena are natural reciprocals in the active and passive voices.

The development in the fish of a rhythmical system of motion responsive to the rhythm impressed upon it by its persistent environment and duly adjusted to it in pulse and force, is a

natural mode of neutralizing the current force and securing stability of position or motion against the current, as desired. Beyond question the form and the movement of the typical fish are admirably adapted to motion in static water and that has been thought a sufficient reason for the evolution of the form, and so possibly it may be, but fishes in static water have not as uniformly retained the attenuated spindle-like form and the extreme lateral flexibility as have those of running water. Among these latter it is rare that any great departure from the typical "lines" and from ample flexibility has taken place, while it is not uncommon in sea fishes. Among the latter not a few have lost both the typical form and the flexibility. The porcupine-fish, the sea-horse, the flounders, and many others are examples of such retrogressive evolution, which is doubtless advantageous to them within their special spheres in quiet waters, but would quite unfit them for life in a swift stream. And if the view be extended to include the low degenerate forms, like the Ascidians, that are by some authors classed as chordates, the statement finds further emphasis.

It is not difficult for the imagination to picture a lowly aggregate of animal cells, still plastic and indeterminate in organization, brought under the influence of a persistent current and caused to develop into determinate organization under its control, and hence to acquire, as its essential features, a spindle-like form, a lateral flexibility, and a set of longitudinal side-muscles adapted to rhythmical contractions, since these are but expressions of conformity and responsiveness to the shape and movement normally impressed by the controlling environment upon plastic bodies immersed in it. The necessity for a stiffened axial tract to resist the longitudinal contractions of the side muscles and thus to prevent shortening without seriously interfering with lateral flexibility, is obvious and is supplied by a notochord. Thus, by hypothesis, the primitive chordate form may be regarded as a specific response to the special environment that dominated the evolution of a previously indeterminate ancestral form.

That some primitive animal aggregate far back in pre-Cambrian time should have found refuge from marine persecution or competition in the sweet running water that entered the sea at so many points, and should have evolved on lines in strict conformity with the dominant force of its new environment does not seem improbable.

If such were the origin of the vertebrate type, its subsequent history and the peculiar phases of fossilization previously discussed are natural sequences.

Distribution from river to river would be slow but inevitable, without the aid of the bizarre agencies of water-fowl, whirlwinds, etc., sometimes appealed to in modern instances. The degradation of the land by streams involves inevitably much piracy, and at the stage of capture the two streams are united for a certain period; and for a still longer period they relieve each other of surplus waters in times of local floods which happen to affect one basin more than the other. Measured by the time requisite for fish migration, these periods of continuous and occasional communication are long. The event itself is, to be sure, infrequent. But in the history of a river basin, the piracy of some one or another of its numerous branches interlocking with the branches of neighboring basins is probably not especially rare. In the next geological period the number of piracies between the headwaters of the Mississippi, the St. Lawrence, the Hudson Bay system, and the Mackenzie will certainly not be few, and before the Cordilleran tract is base-leveled, it may safely be affirmed that piracies at many points will have furnished a migratory tract between the river systems of the interior and those of the Pacific.

Certain attitudes of the sea to the land develop lagoons and sounds behind spits, fringing inlands, and barrier tracts, and if the land be growing at the expense of the sea, the waters of these lagoons and sounds often become wholly cut off from the sea and so pass from the salt to the fresh condition, and thus afford a means of migration from river to river near their mouths. The attitudes which favor this kind of communication occur

inevitably in the changing relations of land and sea that attend the normal progress of geologic periods. Thus, on the headwaters by piracy and along the sea by lagoons, there are systematic sources of intercommunication by which fresh-water faunas may migrate from basin to basin and may thus occupy quite fully their appropriate domain without dependence upon accidental means or coast-wise communication by temporary entrance of the sea, which may be a resource in some cases. Measured by geologic periods, these means of migration are doubtless sufficiently frequent to be altogether adequate.

The extensions and the changes of domain thus provided to the hypothetical primitive chordate organism may be assumed to have sufficed for its expansion and differentiation through a long period without giving rise to any such degree of overcrowding as to force it to take to the sea for relief; and such intrusions upon the sea as occurred during this initial era may be regarded as individual and accidental.¹ If this be so, it may be inferred that even after the primitive chordates had become differentiated into the ancestral classes, and even into the main ordinal types of the fishes as we now know them paleontologically, and had also attained some measure of induration of parts, the preservation of these parts in the sea sediments would be rare; and this is in accord with experience.

In time, however, the streams must inevitably have become overstocked and a severe struggle for existence must have ensued attended by the acquisition of organs of attack and defense; and at length there must have been an irruption into the sea to avoid the greater enemies and the stronger competition at home. To such an irruption is assigned the remarkable apparition of agnathous and gnathous fishes at the close of the Silurian in varied type and clothed in full armor, expressing the urgency of the competition; though a notable part of the

¹ From early individuals that failed to hold their place in the streams for any reason, and succeeded in maintaining themselves in the sea to which they were carried; there may have sprung the lower chordate types like the ascidians and Balanoglossus, if they really belong to the vertebrate phylum.

apparition, it must be observed, was due to the exceptional preservation of the land record. Thereafter, by interpretation, the habitats of both the Agnatha and the Pisces were more general and varied, a portion taking permanently to the sea, and a portion remaining in the land waters, while a third portion migrated between the two. The well-known habit of many of the last to return to the swift inland streams to initiate each new generation is suggestive of ancestral conditions. The sharks, the hag-fishes and many Teleostomes represent divisions that became permanently sea faring. The lung-fishes (Dipnoans), the old-type Crossopterygians, a part of the lampreys, and many others seem to have mainly adhered to the fresh water, at least their present representatives now frequent these waters, either exclusively or in the main. The fossil record of this latter group, throughout the later geologic ages, is well nigh as scant as that previous to the Devonian, and this would seem to be a very significant fact. The lampreys seem to have been ancestrally represented in the Devonian by the little *Palæospondylus gunni* recently found in beautiful preservation in the Achanarras quarry in North Scotland, where conditions for the preservation of fresh-water deposits were exceptionally good. After this single appearance the lamprey type was lost to sight until modern times revealed its probable descendants in the lamprey of our present waters. In like manner, the Dipnoans, after a notable record in the Devonian and Carboniferous periods, where fresh-water life was exceptionally preserved, nearly disappeared from the record, but are now found in three forms, one in each of the three southern continents, Africa, Australia, and South America. So, too, the singular Crossopterygians, though their deployment may have been wider, after a fine display in the Devonian and Carboniferous, passed into a decline in the early Mesozoic and disappeared in the Lias, but are now found in the fresh waters of Africa. Special interest attaches to the Dipnoans and Crossopterygians as the probable ancestors, or the nearest known kin to the ancestors of the amphibians, and through them, of all reptiles, birds, and mammals, because it

carries a certain measure of presumption that the amphibians were fresh-water derivations.

In this larger application of the interpretation herein suggested, the chordate phylum is made to be essentially from first to last a terrestrial race, whose main habitat was the land waters and the land itself, though still a race that sent its offshoots down to sea from time to time from the mid-Paleozoic onwards.

The large hypothetical element in the foregoing interpretation is sufficiently evident and needs neither word of caution nor apology. The problem at present admits of no other than hypothetical treatment. The discussion is merely the attempt of a geologist to interpret from the geologic side the imperfect data that bear obscurely on the habitat of the early vertebrates.

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